

# **DIEL TRENDS IN THE MESOPELAGIC BIOMASS COMMUNITY OF THE NORTHWESTERN HAWAIIAN ISLANDS OBSERVED ACOUSTICALLY**

BY

MARC O. LAMMERS<sup>1</sup>, RUSSELL E. BRAINARD<sup>2</sup>, AND WHITLOW W.L. AU<sup>1</sup>

## **ABSTRACT**

The nighttime mesopelagic biomass occurring on and near six banks in the Northwestern Hawaiian Islands was investigated using a ship-based EK60 scientific echosounder. The locations investigated included French Frigate Shoals, Maro Reef, Lisianski Island/Neva Shoals, Pearl and Hermes Atoll, Kure Atoll, and Midway Atoll. Surveys were designed to sample parallel and/or shore-normal at each site during different times of the night and during the day. A strong diel trend exists in the presence of midwater sound-scattering biota at all six locations visited. Dense communities of organisms accumulate on the edges of each island and the associated banks at night. The highest densities of organisms tend to occur in waters 30 meters or deeper, but significant increases in biomass were also observed at shallower depths. There was considerable temporal and spatial heterogeneity in the occurrence of the biota observed both between and within locations sampled. The biological composition of the observed biota is presently unclear but it resembles the mesopelagic boundary community that occurs in neritic waters off the Main Hawaiian Islands. The nightly influx of this biota into shallow waters is likely a significant, though poorly understood, component of these islands' reefs and nearshore ecosystems.

## **INTRODUCTION**

Sound-scattering layers (SSLs) are communities of organisms composed of various combinations of zooplankton, planktonic larvae, and micronekton. SSLs are found in many parts of the world's oceans and are characterized by a diel vertical migration from daytime subphotic habitats into surface waters at night. Vertically migrating SSLs are an important trophic link in pelagic food webs because they promote a downward transfer of energy from epipelagic waters into the deeper (>500 m), mesopelagic layers of the ocean (Roger and Grandperrin, 1976).

In the Main Hawaiian Islands (MHI), an island-associated SSL occurs that is known as the Mesopelagic Boundary Community (MBC) (Reid et al., 1991). This is a community of micronekton specifically adapted to the boundary region between the neritic and oceanic habitats. This community is made up of at least 23 species of fish,

---

<sup>1</sup>Hawaii Institute of Marine Biology, P. O. Box 1106, Kailua, HI 96834 USA, E-mail: lammers@hawaii.edu

<sup>2</sup>NOAA Pacific Islands Fisheries Science Center, 1125B Ala Moana Boulevard, Honolulu, HI 96814 USA

shrimp, and squid in 12 families. During the day, the MBC is found in waters 400-700 m deep along the slopes of the islands, while at night it rises to within 10 m of the surface.

Recent work on the MBC has demonstrated that, in addition to migrating vertically at night, this community also moves horizontally towards shallower inshore waters (Benoit-Bird et al., 2001). This net diagonal movement begins shortly before sunset and reaches its shallowest point at around the midpoint of the night. The MBC then reverses its movement so that it is back in deeper offshore waters by sunrise. The shallowest depth reached by this migration is presently still unknown, but acoustic observations have detected the MBC in waters with a bottom as shallow as 30 m (Benoit-Bird and Au, 2004), and it is thought that it enters even shallower depths.

The influx of boundary community biomass into coastal waters on a nightly basis remains a poorly understood component of Hawaii's neritic habitat. Stomach analyses of tuna (He et al., 1997), billfish (Skillman, 1998), bottomfish (Haight et al., 1993), and spinner dolphins (Norris et al., 1994; Benoit-Bird, 2004) have shown that boundary community prey represent an important component of their diets. In addition, the occurrence of the MBC in waters shallow enough to overlap with coral reefs raises the possibility that a significant trophic relationship may also exist with this community between these two communities.

Reid et al. (1991) suggested that boundary communities are likely to occur globally in regions where land-associated mesopelagic species are found and that, consequently, an important, but still poorly understood ecological relationship exists between oceanic and island-associated near-shore habitats. To examine this possibility over a broad geographic scale, the occurrence of mesopelagic biomass near islands and atolls in the Northwestern Hawaiian Archipelago was investigated using ship-based echosounders. The objectives of this work were to establish whether diel migrations of biota into neritic waters are as common around the atolls of the Northwestern Hawaiian Islands (NWHI) as they are around the main Hawaiian Islands (MHI), and secondly, whether this nightly influx overlaps with coral reef habitat.

## METHODS

The occurrence of the MBC and other mesopelagic biota was investigated acoustically using two Simrad EK60 echosounders operating at 38 kHz and 120 kHz. Surveys were conducted using the NOAA ship *Oscar Elton Sette* during the 2003 NWHI Reef Assessment and Monitoring Program (RAMP) cruise, between 12 July and 17 August. Both EK60 frequencies were set to operate at the maximum ping rate relative to the detected bottom, a pulse duration of 0.256 ms, a transmit power of 1000 Watts, a beam angle (-3 dB) of 7.1 degrees, and a transducer gain of 24 dB at 38 kHz and 25.1 dB at 120 kHz. Both sounders were calibrated in September of 2004 and again in March of 2005. Calibration values remained consistent within 0.5 dB.

Six locations in the NWHI Archipelago were examined. These were: French Frigate Shoals (N23°45' N latitude, W166°10' W longitude), Maro Reef (N25°25' N

latitude, W170°35' W longitude), Neva Shoal/Lisianski Island (N26°04' N latitude, W173°58' W longitude), Pearl and Hermes Atoll (N27°50' N latitude, W175°50' W longitude), Midway Atoll (N28°12' N latitude, W177°22' W longitude), and Kure Atoll (N28°25' N latitude, W178°20' W longitude). Acoustic surveys were conducted during a 6-hour time window at night and a 1-2 hour opportunistic time window during the day. Each location was surveyed over a period of either 2, 3, or 4 days and nights. A set of 2 to 4 systematic transect lines ranging in length from 3 to 6 nautical miles were acoustically sampled at a speed of 5-6 knots three times during the night (Fig. 1). The placement of transect lines was balanced between the study's objectives, cruise logistics related to daytime diver-based operations, and local weather and sea conditions.

Different times relative to the middle of the night were examined to establish whether a net movement of biomass across and/or along transects took place. The middle of the night was defined as the halfway point between sunset and sunrise, the time of which changed with increasing longitude. Each transect was also sampled once during the day as cruise logistics permitted to give a day/night comparison. In addition, to provide a comparison between data obtained in the NWHI and the boundary community known to occur in the MHI, a single nighttime transect along the leeward coast of the island of Oahu was conducted during a separate cruise on 9 April, 2004 with the same vessel.

Data were analyzed using Echoview 2.25. To examine the relative abundance and distribution of biomass between and along transect lines, the sampled water column was divided into cells 100 m long by 5 or 10 m deep (deeper waters were divided into deeper cells). Twenty percent of all the cells from each transect down to a depth of 180 m were randomly selected as the basis for statistical comparison between times. Cells deeper than 180 m were excluded from the analysis due to the presence of time-varying gain-related noise with increasing depth.

The mean volume backscattering strength ( $S_v$ ) for each cell was used as a relative measure of biomass (Throne, 1971; MacLennan and Simmonds, 1992). Changes in  $S_v$  values were used as indicators that the total biomass and/or the relative composition of biomass had changed over time and space. Larger (less negative)  $S_v$  values are indicative of an increase in biomass density, a shift in the species composition towards those with higher target strength, or an increase in target strengths due to changes in animal orientation or swim bladder volumes, or a combination of these (Deemer and Hewitt, 1995) (Fig. 2). To represent the relative occurrence of biomass as a function of time, depth, and location along transects, each transect was divided into 3-5 segments, and the cells for each segment were averaged into depth bins of 5, 10, or 30 m.

Prior to calculating  $S_v$ , the data were visually inspected and pre-processed using Echoview's data exclusion utility to remove extraneous noise artifacts, such as false echoes arising from water turbulence related to the ship's motion. In addition, the top 10 m of each transect was rejected from the analysis to avoid the confounding influence of wave-induced surface bubbles. Volume backscatter was calculated only for waters 2 m or more above the bottom.

## RESULTS

In Table 1 we describe the statistical relationship between the daytime and nighttime occurrence of mid-water biota at the six locations surveyed. In all cases, more biomass occurred in the water column at night than during the day. There was considerable variability in the diel occurrence of biomass both temporally and spatially. This was the case within as well as between locations. More backscattered acoustic energy was consistently received with the 38- kHz echosounder than the 120- kHz system. Consequently, the summary findings detailed below for each location reflect only the 38- kHz data. A comparative analysis of the results obtained using both frequencies will be the subject of a future publication.

### French Frigate Shoals

Three acoustic transects were conducted at French Frigate Shoals (FFS) (Fig. 1A). Transect A was adjacent and parallel to the reef flat, transect B was centrally located on the main bank of the shoals, and transect C was placed parallel to the slope of the bank. The diel difference was greatest along transect C, where dense layers of biota accumulated throughout the night (Table 1). The relative diel difference was approximately equal along transects A and B, but A had a greater absolute density of biomass during both daytime and nighttime.

For further analysis, each transect was divided into five equidistant 1.9- km segments. Table 2 reveals where biomass occurred as a function of depth and time. Along transects A and B, the occurrence of nighttime biota increased throughout the water column, but especially near the bottom 5-10 m. Increases were not homogeneous, but rather occurred in localized maxima or 'patches.' The densest patches along both transects occurred during the period preceding the middle of the night (2200h) and began to dissipate by 0300h. The increases in biota observed along transect C differed in that patches of biomass occurred as localized layers in the water column. Between two and three distinct layers occurred simultaneously during the early (2200h) and middle (0030h) periods of the night between 50 and 150 m. During the late period (0300h), distinct layers were still present but occurred deeper. Throughout the night, the densest aggregations occurred where a layer would come into contact with the bottom along the edge of the slope (Table 2, transect C, segment 'Edg').

To determine whether nocturnally present biota migrate horizontally from the slopes of the bank onto the shallows near the reef flat, we considered the relative occurrence of biomass in relation to the time of night. We expected that, if horizontal migration across the bank takes place through the night, two roughly equivalent local maxima of relative abundance would occur along transects B and C during the first and third quarters of the night (2200h and 0300h, respectively), and a local maximum would be observed along transect A during the midpoint of the night (0030h) (Fig. 3A). This was not the case, however (Fig. 3B). A similar analysis of relative biomass occurring along (rather than across) each transect as a function of time also did not match the predictions of large- scale horizontal movement, at least not within the time frame examined.

## Maro Reef

Maro Reef was surveyed over the course of two days and nights, during which two shoal-normal transects were systematically sampled (Fig. 1B). Both transects initiated adjacent to the shallow reef flat and extended past the slope of the bank. For analysis, each transect was divided into five segments based on depth and distance from the reef flat: three 'shallow- bank' segments (length = 2.1 km for transect A, 2.9 km for transect B), an 'edge- of- bank' segment (length = 1.6 km for transect A, 1.2 km for transect B), and a 'slope- of- bank' segment (length = 1.5 km for transect A, 0.8 km for transect B). Biomass increases occurred throughout the length of both transects, but the highest densities accumulated on the 'edge- of- bank' segment in water between 30 and 90 m deep (Table 2). The layer was densest between 30 and 60 m deep where it impinged on the rising slope of the bank, but it extended well onto the bank along the 10 m closest to the bottom. This distribution pattern was relatively consistent throughout the three nighttime periods sampled, suggesting that only limited, if any, net horizontal movement normal to the reef flat took place within the time frame examined.

## Neva Shoal/Lisianski Island

Three transects parallel to the reef flat were sampled at Neva Shoal over three days and nights (Fig. 1C). As at FFS, transect A was adjacent and parallel to the reef flat, transect B was located centrally on the main bank of the shoal, and transect C was placed parallel to the slope of the bank. Significant nightly increases in biomass were measured on transects A and C (Table 1). Transect B was not sampled during the day due to operational restrictions with the ship.

The difference in daytime vs. nighttime biomass density was considerably greater along the slope of the bank than near the reef flat. As was observed at FFS, there were predominant increases in biomass towards the bottom half of the water column near the reef flat (transect A), comparatively less biota along the middle of the bank (transect B), and a distinct layering of biomass centered between 30 and 90 m deep along the slope of the bank (transect C). As at Maro Reef, the layers found along the slope were densest where they impinged on the rising slope of the bank. An examination of the occurrence of biomass between and along transects in relation to the time of night, as described for FFS, also did not yield any clear evidence of net horizontal movement across the bank within the time frame considered. During the daytime, most of the remaining biota occurred in the middle of the water column, towards the southern ends of both transects A and C.

## Pearl and Hermes Atoll

Pearl and Hermes Atoll was surveyed during four days and nights. Cruise logistics and favorable weather allowed four transects to be conducted on three sides of the Atoll (Fig. 1D). Transects A and B were shore-normal on the northeastern and southwestern corners of the Atoll, respectively. Both transects initiated adjacent to the

shallow reef flat and extended past the slope of the bank. For analysis, each transect was divided into five 1,400- m segments representing different depth strata and distances from the reef flat. These were labeled using the same nomenclature employed at Maro Reef.

Transects C and D were both on the southern side of the Atoll, parallel to shore and to one another. Transect C extended over a long segment of both declining and inclining slope, dropping to a depth of approximately 650 m in between and leveling off into a bank on the western end. For analysis, transect C was divided into four depth strata: a 'slope-of- bank' ('Slo') segment, an 'edge- of- bank' ('Edg') segment, and two 'shallow- bank' ('Shb') segments. Transect D was offshore of C and was mostly over water greater than 1,000 m deep. For analysis, it was divided into a 'deep- water' segment, a 'slope- of- bank' segment, and an 'edge- of- bank' segment.

Transect A had the lowest nighttime Sv values of the four, but exhibited a distinct layer of biomass centered at the 31-60- m depth range throughout the night (Table 2). This layer occurred along the entire transect, but was densest mid-water along the 'edge' and 'slope' segments. A second, more localized layer was associated with the bottom below approximately 60 m, primarily along the middle 'shallow- bank' segment (Table 2, transect A, Shb2).

Transect B exhibited a similar distribution pattern as transect A, but with a considerably higher density of biomass along the shallowest two segments of the bank (Table 2, transect B, Shb1 and Shb2). In addition, the dense patch of biota occurring along the middle 'shallow- bank' segment (Shb2) persisted into the day, although it disassociated itself from the bottom and became concentrated in a layer centered approximately 20 m above the bottom.

A dense layer of biota centered between 31 and 60 m deep occurred along the length of transect C. This layer was densest near the bottom of the 'edge' and first 'shallow- bank' ('Edg' & Shb1) segments during the middle of the night. The layer scattered somewhat and descended deeper as the night wore on, but a notable density of biomass remained in both 'shallow- bank' segments (Shb1 & Shb2) during the pre-dawn hours and persisted there during the day.

Transect D was dominated by deeper waters than transects A, B and C. However, as with the other three transects, a layer of biota centered between 31 and 60 m deep occurred there during the majority of the night. Also consistent with the other three transects was the higher concentration of biomass at the lower depths of the 'edge' segment. In contrast with transects C and B, however, low densities of 'edge'-associated biota remained during the day.

## Midway Atoll

Two transects parallel to the southern slope of Midway Atoll were sampled during two days and nights (Fig. 1E). Transect A extended from the center of the Atoll's southwestern bank to near the entry channel into the lagoon. The bottom along this transect gradually sloped upward from a maximum depth of 97 m on the western end to a minimum depth of 46 m on the eastern end. Transect B ran parallel to A along the edge and slope of the Atoll. The depth along transect B varied widely between 423 m and 91 m.

Transect A exhibited a nocturnal increase in biomass throughout the water column, but especially towards the eastern end below 20 m. The abundance of biota remained high throughout most of the night and began to decrease prior to sunrise (0530h). It persisted the longest towards the eastern end of the transect, which was adjacent to a steeper slope than the western end and was therefore characteristic of the 'edge' bathymetry described for other locations in the Archipelago.

Transect B differed in the distribution of biomass between the western and eastern end. The western end was characterized by a distinct biomass layer near the surface and an accumulation near the bottom, separated by low densities in the middle of the water column, particularly at 0300h. On the eastern end, the surface layer became denser and reached deeper, but no accumulation near the bottom was observed. Toward sunrise, the distribution pattern changed considerably, with the bulk of the biota occurring at the lower depths of the western end, most likely representing the downward phase of the diel migration cycle.

#### Kure Atoll

Kure Atoll was surveyed during two days and nights. Two transects were sampled parallel to the Atoll's western slope (Fig. 1F). Transect A was the shallower of the two with nearly homogeneous depths. Transect B was parallel to A, approximately 2.3 km further offshore. The bottom of transect B sloped upward on the northern end, but was roughly constant in depth towards the southern end.

A nocturnal increase in biomass occurred throughout the water column along transect A during the middle of the night (0030h) and gradually decreased in density as the night wore on, particularly along the bottom half of the water column (Table 2). Transect B was characterized by dense aggregations below approximately 100 m and a secondary, more diffuse layer towards the surface. The densest patches observed along transect B occurred during the latter part of the night (0300h) along the northern end. A distinct patch persisted there into the last phase of the night (0530), but was entirely gone by daytime.

#### Waianae, Oahu

A single 6.3- km transect was conducted parallel to the northern Waianae coast of Oahu during the middle of the night in waters between 45 m and 120 m deep. The average volume backscattering strength calculated for Waianae was near the median of the distribution of all the NWHI transects for both frequencies (Table 1). The concentration of biomass was patchy, with a distinct mid-water layer occurring towards the northern end and a more bottom-associated layer towards the southern end. The highest observed density was found along the edge of a descending slope towards the southern end. The density and distribution pattern of the biota encountered off Waianae was not distinct in any notable way from the range of the patterns observed in the NWHI.

## DISCUSSION

The study's primary objective was to answer the question: are diel migrations of biota into neritic waters common in the NWHI? We indicate that they are. Increases in nocturnal mid-water biomass were noted at all locations and along each transect surveyed. However, considerable spatial and temporal heterogeneity characterized the occurrence of this biota. Each site exhibited localized maxima in densities that tended to peak during the middle of the night and gradually subside prior to sunrise. During the day, most locations, regardless of depth, exhibited a substantial decrease and even total absence of the sound-scattering biota observed at night.

Although there was much variability, certain spatial patterns in the occurrence of this nighttime biota did emerge. The most consistent and dense aggregations were observed on and near the edges of the slopes of the atolls and shoals visited. The band of water between 30 m and 90 m deep nearly always had one or more distinct layers associated with it, usually throughout the night. These layers typically extended well beyond the slope, both offshore and towards the shore or reef flat. Interestingly, the layers often had well-defined upper boundaries, usually below 20 m deep. This may be tied to avoidance of light reflected from the moon, which can lead to greater predation (Gliwicz, 1986; Gal et al, 1999). Conversely, there appeared to be no avoidance of the benthos, although this changed during the day when, on the few occasions where a layer did persist into daytime hours, there was always a clear separation from the bottom (e.g., Pearl & Hermes Atoll transect B).

The second major objective was to determine whether the migratory biota observed near the slopes of atolls enters coral reef habitat. This point remains unresolved. There was clearly a nocturnal influx of biota into the water column at sites with depths commonly associated with coral reef habitat (~20-40 m), such as transect A at French Frigate Shoals (FFS). However, the data obtained did not reveal an identifiable, horizontally migrating 'front' of organisms that might account for this biomass, as has been observed in the MHI (Benoit-Bird et al 2001; Benoit-Bird and Au, 2004). Therefore, we presently cannot exclude the possibility that at least some of the biota observed arose from within or near the bottom locally. Benoit-Bird and Au (2004) have reported that the average horizontal migratory rate of micronekton off Oahu is  $1.7 \text{ km h}^{-1}$ . So, it is possible that biota observed over reef habitats within 2-3 km of an atoll's slope migrated there from deep waters quickly following sunset, and therefore did not appear as a moving front during the time frame we sampled. However, this is unlikely for the interior of large banks such as FFS and Maro Reef, where the reef flat is more than 10 km from the bank's slope.

Regardless of origin, the finding of consistently higher nocturnal biomass densities over reef habitat is important because it suggests that traditional daytime biological assessments may not capture all the trophic relationships present on the reef and may under-represent certain groups. This is relevant to efforts aimed at creating ecological models for the NWHI. For example, Friedlander and DeMartini (2002) reported that over 54% of the total fish biomass observed on reefs in the NWHI consists of apex predators, raising the intriguing question of how so many top-level consumers



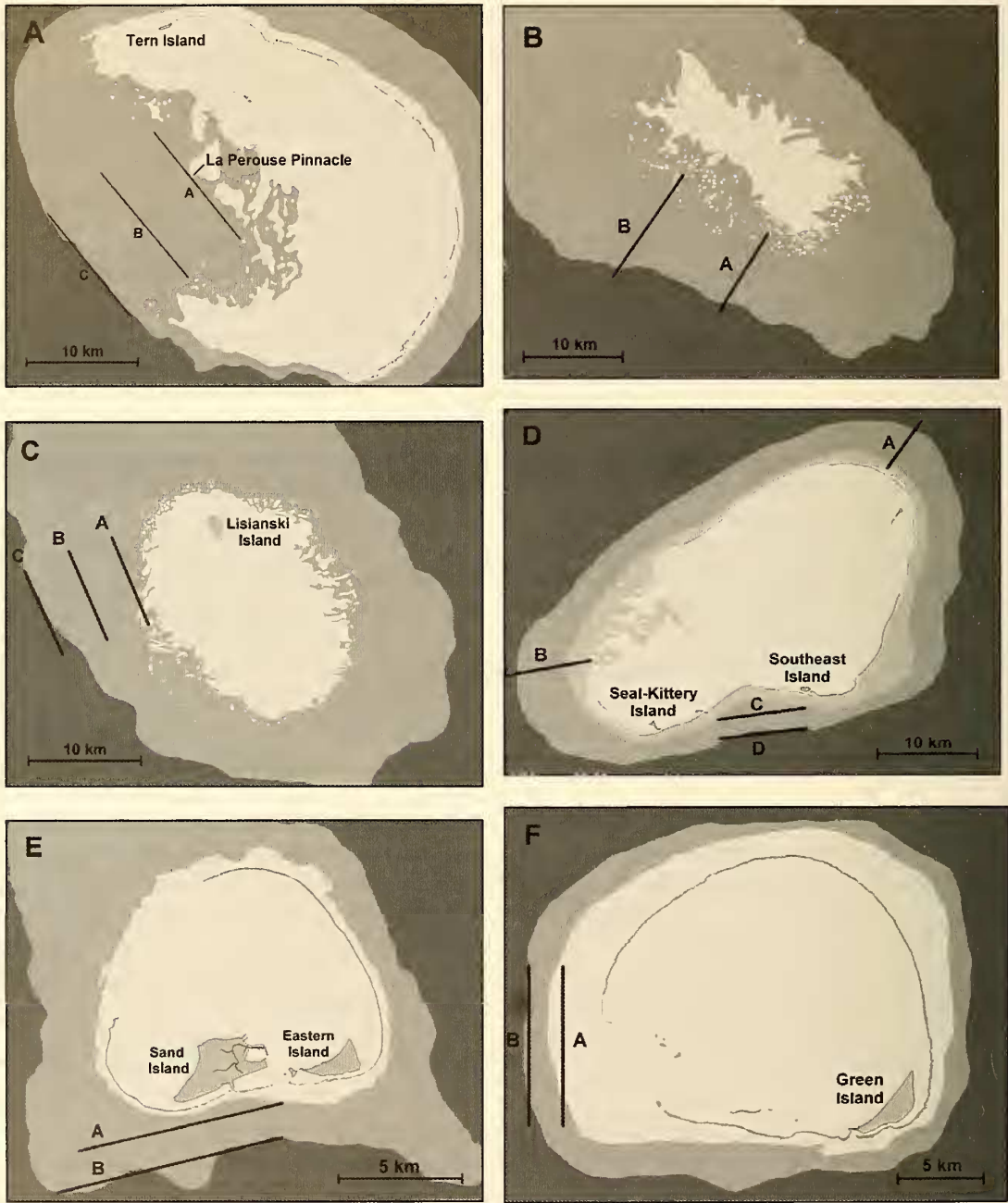
are trophically supported. A part of the answer may lie with the nocturnal influx of biota reported here.

Another unresolved issue is the taxonomic makeup of the biota observed. Logistical restrictions did not allow trawling for samples during acoustic data collection. Consequently, we can say relatively little about the identity of the organisms that occur at the various locations sampled. The fact that more backscattered acoustic energy was consistently received with the 38- kHz echosounder (vs. 120-kHz) than 120 kHz is suggestive of micronekton rather than zooplankton, since the smaller zooplankters would be expected to reflect more acoustic energy at the higher of the two frequencies (MacLennan and Simmonds, 1992). In addition, the fact that the limited data obtained off the Waianae coast of Oahu fell in line with mean Sv values from the NWHI further points to biota related to the mesopelagic boundary community.

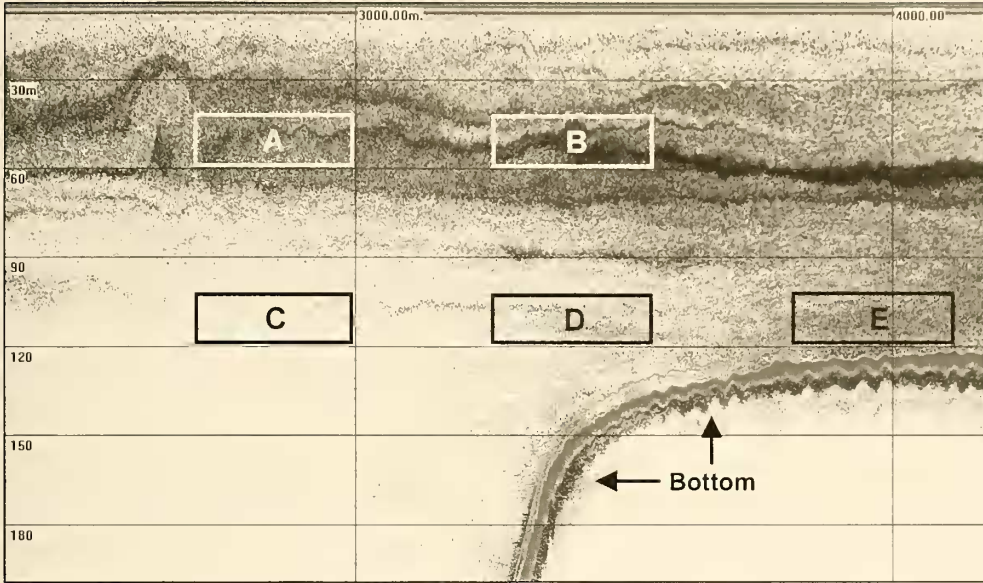
In summary, it is reasonable to conclude that the nocturnal composition of biota in neritic waters off atolls and islands in the NWHI Archipelago is substantially different from what is observed there in the daytime. This should be carefully considered when planning ecosystem assessments or trying to model trophic relationships based on observed biomass. To better understand the ecological importance of these diel migrations, future surveys will need to resolve questions about the biological makeup of biota at different sites. In addition, engaging in long-term monitoring of migration trends and correlated oceanographic conditions will yield important insights into the dynamics of these communities and possibly provide information on long-term patterns in the health of neritic ecosystems.

#### ACKNOWLEDGEMENTS

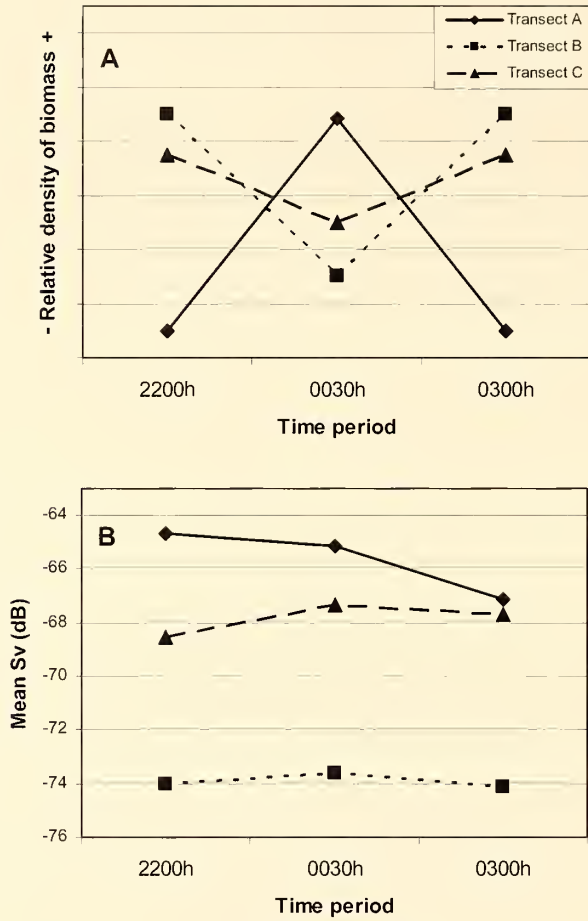
We would like to thank the officers and crew of the *Oscar Elton Sette* who made every effort to accommodate the scientific needs of the study. Phil White in particular provided invaluable assistance. An anonymous reviewer provided helpful commentary on an earlier draft of the manuscript. This is HIMB publication #1201.



**Figure 1.** Acoustically sampled transect lines at French Frigate Shoals (A), Maro Reef (B), Lisianski Island/Neva Shoal (C), Pearl and Hermes Atoll (D), Midway Atoll (E), and Kure Atoll (F).



**Figure 2.** Nocturnal aggregation of biota observed with the 38-kHz echosounder along transect C at Pearl and Hermes Atoll. The figure illustrates the relationship between the relative density of biomass and volume backscattering strength (Sv). Cell A = -61.5 dB; Cell B = -56.3 dB; Cell C = -73.4 dB; Cell D = -67.3 dB; Cell E = -64.3 dB.



**Figure 3.** Relative biomass density along the transect at FFS. For a hypothesized nocturnal migration across the bank, the expected pattern (A) was not observed (B).

Table 1. Table of nocturnal vs. diurnal mean Sv values measured for each transect sampled. Statistical comparisons are based on two-sample t-tests.

	Transect	Mean Sv (dB) 38 kHz				Mean Sv (dB) 120 kHz			
		Day	Night	$\Delta$	P	Day	Night	$\Delta$	P
French Frigate Shoal	A	-70.06	-65.15	-4.91	< 0.001	-74.45	-69.67	-4.78	< 0.001
	B	-77.94	-73.58	-4.36	< 0.001	-81.84	-76.21	-5.63	< 0.001
	C	-74.64	-67.35	-7.30	< 0.001	-83.43	-76.54	-6.88	< 0.001
Maro Reef	A	-77.35	-69.19	-8.16	< 0.001	-84.41	-77.11	-7.30	< 0.001
	B	-75.31	-69.58	-5.73	< 0.001	-82.79	-76.35	-6.43	< 0.001
Lisianski / Neva Shoal	A	-73.14	-70.99	-2.16	0.017	-73.86	-70.39	-3.46	0.006
	B	N/A	-72.34	-	-	N/A	-75.10	-	-
	C	-74.57	-64.93	-9.64	< 0.001	-78.13	-71.62	-6.51	< 0.001
Pearl & Hermes Atoll	A	-76.36	-69.74	-6.62	< 0.001	-80.67	-76.28	-4.39	< 0.001
	B	-72.96	-68.45	-4.51	0.007	-79.15	-76.28	-2.87	0.013
	C	-74.93	-66.61	-8.31	< 0.001	-82.26	-74.41	-7.86	< 0.001
	D	-77.55	-68.96	-8.59	< 0.001	-84.91	-77.62	-7.28	< 0.001
Midway Atoll	A	-75.35	-64.79	-10.56	< 0.001	-74.76	-68.95	-5.82	< 0.001
	B	-77.57	-69.42	-8.14	< 0.001	-84.00	-77.38	-6.62	< 0.001
Kure Atoll	A	-74.38	-67.95	-6.42	< 0.001	-76.43	-71.68	-4.75	< 0.001
	B	-76.91	-70.78	-6.13	< 0.001	-84.41	-77.83	-6.58	< 0.001
Waianae, Oahu	A	N/A	-67.86	-	-	N/A	-74.30	-	-

Table 2. The volume backscattering strength (Sv) measured along each transect as a function of water column depth during different times of the night and during daytime. Gray-scaled cells represent relative acoustic backscatter at 38 kHz. Darker cells represent greater backscatter. *Shb*: shallow bank; *Slo*: slope; *Edg*: edge; *Deep*: > 500 m deep. A solid (\_\_\_\_) base indicates the cell includes the bottom, a dashed ( \_ \_ ) base indicates the cell partly includes the bottom, and a dotted (.....) base indicates the cell does not include the bottom.

<b>French Frigate Shoals</b>																									
Transect A					2200					0030					0300					Day					
Depth (m)	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5
10-15	-68.9	-66.9	-67.9	-66.7	-66.0	-67.8	-67.4	-67.0	-64.3	-64.5	-67.5	-67.6	-67.8	-65.9	-65.4	-68.2	-67.3	-66.3	-65.9	-74.9	-68.2	-67.3	-66.3	-65.9	-74.9
16-20	-69.0	-65.8	-66.1	-65.3	-65.7	-66.9	-66.1	-66.5	-64.1	-63.6	-66.6	-67.3	-67.4	-66.1	-65.3	-66.9	-67.6	-67.6	-69.0	-68.0	-66.9	-67.6	-67.6	-69.0	-68.0
21-25	-64.6	-61.5	-61.2	-60.3	-63.6	-64.8	-64.4	-65.8	-62.7	-62.1	-67.0	-68.4	-68.2	-67.9	-68.3	-70.9	-75.5	-73.2	-70.4	-72.1	-70.9	-75.5	-73.2	-70.4	-72.1
Avg. depth	← 24.1 →																								
<b>Transect B</b>																									
NW					SE					0030					0300					Day					
Depth (m)	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5
10-15	-77.1	-76.0	-76.5	-70.2	-74.7	-74.6	-74.6	-73.1	-73.5	-77.0	-74.4	-74.8	-75.7	-75.5	-75.2	-73.1	-73.1	-75.1	-74.0	-80.0	-73.1	-73.1	-75.1	-74.0	-80.0
16-20	-77.1	-75.5	-76.6	-72.0	-72.5	-73.9	-74.1	-73.6	-72.6	-76.7	-73.9	-73.7	-74.7	-74.7	-73.6	-76.5	-75.7	-77.3	-77.1	-82.3	-76.5	-75.7	-77.3	-77.1	-82.3
21-25	-76.3	-74.1	-75.3	-69.9	-69.4	-73.5	-73.5	-73.8	-72.6	-75.0	-72.9	-73.0	-74.4	-74.6	-73.6	-79.6	-79.5	-78.9	-80.8	-83.8	-79.6	-79.5	-78.9	-80.8	-83.8
26-30	-73.7	-73.4	-74.3			-71.3	-73.2	-73.1			-72.4	-73.2	-74.9			-75.5	-75.7	-82.1			-75.5	-75.7	-82.1		
Avg. depth	← 30.8 →					27.2 23.5																			
<b>Transect C</b>																									
2200					0030					0300					Day										
Depth (m)	Slo1	Edg	Slo2	Slo3	Slo4	Slo1	Edg	Slo2	Slo3	Slo4	Slo1	Edg	Slo2	Slo3	Slo4	Slo1	Edg	Slo2	Slo3	Slo4	Slo1	Edg	Slo2	Slo3	Slo4
10-30	-72.0	-71.5	-75.4	-76.7	-73.8	-76.5	-74.2	-74.3	-71.7	-70.5	-70.0	-73.0	-73.5	-71.3	-71.2	-75.3	-72.2	-73.2	-74.4	-74.9	-75.3	-72.2	-73.2	-74.4	-74.9
31-60	-66.9	-66.5	-67.4	-69.8	-70.4	-70.6	-71.0	-67.4	-67.8	-71.4	-66.1	-66.8	-68.2	-70.8	-70.1	-76.4	-75.5	-75.3	-75.0	-75.8	-76.4	-75.5	-75.3	-75.0	-75.8
61-90	-66.1	-66.4	-63.5	-66.5	-67.6	-65.4	-64.1	-64.1	-69.8	-72.2	-66.8	-69.7	-73.2	-73.6	-72.1	-74.9	-73.6	-74.6	-74.8	-77.5	-74.9	-73.6	-74.6	-74.8	-77.5
91-120	-68.6	-61.1	-65.0	-61.6	-60.1	-62.6	-59.9	-62.7	-64.9	-68.0	-64.8	-63.8	-65.5	-67.2	-66.2	-74.4	-74.3	-74.4	-73.7	-75.3	-74.4	-74.3	-74.4	-73.7	-75.3
121-150	-70.5	-61.9	-62.8	-69.1	-63.4	-61.4	-62.1	-64.7	-62.3	-65.6	-63.4	-62.8	-66.2	-63.8	-64.2	-74.4	-70.2	-76.0	-74.4	-75.7	-74.4	-70.2	-76.0	-74.4	-75.7
Avg. depth	239	149	249	175	206																				
<b>Maro Reef</b>																									
Transect A					2200					0030					0300					Day					
Depth (m)	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo
10-30	-72.5	-71.5	-66.8	-66.5	-67.1	-72.4	-68.9	-65.5	-64.8	-66.8	-71.1	-68.5	-68.0	-69.5	-67.1	-81.4	-76.9	-74.1	-70.2	-79.9	-81.4	-76.9	-74.1	-70.2	-79.9
31-60			-61.6	-68.1				-62.5	-70.9				-62.8	-68.2				-70.3	-71.9				-70.3	-71.9	
61-90			-63.6	-69.5				-65.5	-71.2				-61.5	-70.3				-70.2	-77.5				-70.2	-77.5	
91-120				-70.3					-72.3					-70.2				-78.2	-81.7				-78.2	-81.7	
121-150				-70.7					-72.5					-71.6				-81.7	-87.2				-81.7	-87.2	
Avg. depth	← 30.7 →					66.5 39.3																			
<b>Transect B</b>																									
NE					SW					0030					0300					Day					
Depth (m)	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo
10-30	-71.2	-70.5	-67.5	-70.2	-70.4	-72.0	-70.2	-65.9	-70.2	-71.5	-70.7	-69.0	-68.4	-70.6	-72.2	-79.1	-76.8	-75.3	-79.1	-77.3	-79.1	-76.8	-75.3	-79.1	-77.3
31-60				-66.0	-64.2				-61.2	-63.9				-63.0	-66.8				-76.8	-67.4				-76.8	-67.4
61-90				-67.3	-65.4				-65.0	-66.1				-62.6	-66.0				-75.3	-77.1				-75.3	-77.1
91-120				-70.5					-74.3					-69.7				-78.4	-77.1				-78.4	-77.1	
121-150				-75.7					-74.4					-74.9				-79.4	-79.4				-79.4	-79.4	
Avg. depth	← 33.2 →					63.9 32.5																			
<b>Lisianski/Neva Shoal</b>																									
Transect A					2230					0100					0330					Day					
Depth (m)	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5
10-15	-70.2	-69.9	-71.2	-72.0	-72.3	-73.7	-73.6	-72.9	-74.7	-71.6	-74.0	-74.0	-73.6	-74.2	-70.3	-70.5	-72.0	-74.6	-68.1	-67.7	-70.5	-72.0	-74.6	-68.1	-67.7
16-20	-72.1	-70.7	-71.3	-71.9	-72.1	-73.3	-73.4	-72.6	-73.8	-69.2	-73.6	-73.7	-73.2	-73.6	-69.7	-72.7	-74.8	-77.9	-70.1	-67.7	-72.7	-74.8	-77.9	-70.1	-67.7
21-25	-74.7	-71.7	-71.6	-72.0	-68.7	-73.0	-72.7	-71.4	-71.7	-63.7	-73.1	-73.5	-72.2	-71.2	-66.5	-76.8	-79.8	-81.1	-71.5	-67.2	-76.8	-79.8	-81.1	-71.5	-67.2
26-30	-76.1	-71.7	-64.1	-65.3	-70.3	-72.5	-69.2	-63.9	-66.0	-64.0	-72.9	-71.4	-67.2	-64.2	-72.0	-77.6	-74.8	-74.0	-73.3	-76.6	-77.6	-74.8	-74.0	-73.3	-76.6
Avg. depth	← 28.8 →																								
<b>Transect B</b>																									
North					South					0100					0330					Day					
Depth (m)	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5
10-15	-69.9	-72.3	-71.7	-69.6	-68.1	-71.2	-70.5	-71.0	-70.2	-70.6	-71.7	-75.9	-74.8	-75.7	-73.9	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
16-25	-71.4	-73.8	-72.4	-70.0	-68.2	-71.9	-71.6	-71.8	-71.5	-71.9	-71.9	-75.3	-73.4	-72.9	-72.6	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
26-35	-72.1	-72.4	-72.4	-70.5	-65.2	-73.6	-73.5	-73.1	-71.7	-69.6	-71.1	-73.3	-71.7	-70.1	-68.1	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Avg. depth	← 32.0 →																								
<b>Transect C</b>																									
2230					0100					0330					Day										
Depth (m)	Edg1	Edg2	Edg3	Edg4	Edg5	Edg1	Edg2	Edg3	Edg4	Edg5	Edg1	Edg2	Edg3	Edg4	Edg5	Edg1	Edg2	Edg3	Edg4	Edg5	Edg1	Edg2	Edg3	Edg4	Edg5
10-30	-65.1	-65.5	-63.7	-66.2	-66.9	-69.9	-67.2	-66.7	-67.1	-68.4	-73.3	-71.3	-71.8	-72.2	-72.7	-72.0	-72.7	-73.1	-70.4	-72.3	-72.0	-72.7	-73.1	-70.4	-72.3
31-60	-58.9	-59.0	-57.0	-59.2	-60.8	-65.6	-65.6	-63.0	-62.8	-63.2	-66.3	-64.8	-65.7	-65.3	-69.9	-75.4	-75.3	-73.9	-67.6	-69.4	-75.4	-75.3	-73.9	-67.6	-69.4
61-90	-65.0	-59.0				-58.4	-63.5	-59.7			-59.8	-63.5	-56.0			-64.6	-80.4	-80.8			-64.6	-80.4	-80.8		
91-120						-68.4					-66.0					-69.5					-69.5				
Avg. depth	87.7	71.7	67.4	54.7	103																				

**Pearl & Hermes Atoll**

**Transect A**

Depth (m)	2200					0030					0300					Day				
	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo
10-30	-72.5	-71.7	-73.2	-71.8	-71.3	-70.1	-71.3	-72.8	-72.4	-70.9	-71.2	-71.7	-71.0	-71.0	-70.8	79.3	-80.3	-79.0	-78.3	-78.6
31-60	-68.0	-68.5	-67.6	-65.8	-65.9	-68.5	-68.5	-66.7	-66.3	-66.1	-68.7	-69.0	-68.0	-67.1	-67.0	-75.9	-74.6	-74.9	-75.5	-74.4
61-90		-67.8	-68.9		-71.0		-65.3	-69.8		-70.4		-72.1		-72.2			-78.8	-75.5	-76.4	-75.5
91-120				-70.9	-73.3				-72.9	-74.5				-71.5	-72.9				-77.8	-76.6
121-150					-71.5					-71.7					-74.2					-76.9
Avg. depth	48.0	72.0	85.3	103	357															

**Transect B**

Depth (m)	0030					0300					0445					Day				
	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo	Shb1	Shb2	Shb3	Edg	Slo
10-30	-65.8	-64.5	-70.6	-64.0	-67.8	-67.3	-69.5	-71.5	-70.8	-69.3	-70.1	-70.1	-72.6	-69.6	-69.1	-69.2	-64.1	-73.4	-79.4	-81.1
31-60	-57.1	-51.8	-69.8	-65.3	-69.0	-56.5	-68.5	-67.9	-67.0	-68.8	-59.0	-66.2	-68.4	-66.9	-67.7	-68.3	-56.0	-75.0	-76.4	-75.3
61-90		-49.0	-70.2	-70.8	-73.0		-68.4	-73.8	-72.2	-69.4		-53.5	-71.4	-72.2	-73.0		-69.7	-72.4	-78.0	-77.3
91-120				-65.4	-78.1				-73.8	-74.0				-73.4	-74.1				-75.6	-75.5
121-150					-78.9					-77.9					-76.1					-79.1
Avg. depth	26.2	63.0	78.1	105	363															

**Transect C**

Depth (m)	0030				0300				0530				Day			
	Slo	Edg	Shb1	Shb2	Slo	Edg	Shb1	Shb2	Slo	Edg	Shb1	Shb2	Slo	Edg	Shb1	Shb2
10-30	-67.9	-70.2	-65.4	-69.6	-65.8	-65.0	-64.3	-63.9	-62.4	-66.8	-67.5	-69.4	-67.6	-68.5	-66.3	-67.6
31-60	-61.3	-62.8	-61.2	-61.2	-64.3	-63.6	-59.6	-53.7	-67.0	-70.7	-64.3	-66.2	-70.3	-72.4	-68.9	-68.8
61-90	-65.4	-60.0	-56.6		-67.6	-64.0	-56.3		-75.0	-77.7	-70.7		-79.1	-80.4	-77.4	
91-120	-71.0	-62.0		-66.5	-60.3			-75.1	-77.0				-80.1	-80.7		
121-150	-73.6			-71.3				-76.0					-81.4			
Avg. depth	44.1	128	108	46.7												

**Transect D**

Depth (m)	0030			0300			0530			Day			Mean Sv (dB)
	Deep	Slo	Edg	Deep	Slo	Edg	Deep	Slo	Edg	Deep	Slo	Edg	
10-30	-67.0	-68.1	-67.0	-67.0	-66.9	-64.9	-67.4	-69.3	-70.0	-72.6	-75.8	-76.6	>= -63.5
31-60	-65.1	-64.5	-64.8	-64.1	-65.6	-64.6	-68.5	-71.2	-73.7	-75.1	-73.3	-72.4	-63.6 to -66.5
61-90	-68.9	-65.4	-65.7	-66.4	-68.9	-70.9	-75.3	-77.8	-80.6	-78.5	-79.1	-79.6	-66.6 to -69.5
91-120	-72.7	-67.9	-64.0	-68.3	-71.3	-75.8	-75.1	-77.3	-77.8	-79.6	-79.6	-80.1	-69.6 to -72.5
121-150	-77.6	-72.5	-59.4	-73.7	-72.6	-73.8	-76.7	-78.8	-68.9	-80.6	-76.4	-79.3	<= -72.6
Avg. depth	>1000	287	108										

**Midway Atoll**

**Transect A**

Depth (m)	0030					0300					0530					Day				
	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5
10-30	-65.7	-65.8	-67.2	-67.8	-65.5	-65.5	-68.9	-70.7	-64.8	-60.4	-67.0	-68.5	-67.8	-67.1	-65.6	-67.7	-76.9	-64.5	-67.7	-68.3
31-60	-67.7	-64.5	-61.6	-59.5	-58.8	-66.2	-64.5	-64.7	-58.5	-53.6	-71.1	-73.5	-69.5	-63.4	-71.0	-67.4	-69.3	-74.8	-69.5	-76.8
61-90	-65.0	-62.7				-64.2	-61.2				-71.1	-75.0				-75.8	-79.0			
Avg. depth	86.0	69.8	53.9	45.5	43.7															

**Transect B**

Depth (m)	0030					0300					0530					Day					
	Edg	Slo1	Shb	Slo2	Slo3	Edg	Slo1	Shb	Slo2	Slo3	Edg	Slo1	Shb	Slo2	Slo3	Edg	Slo1	Shb	Slo2	Slo3	
10-30	-68.7	-69.3	-65.9	-65.2	-66.3	-66.9	-64.3	-64.9	-65.8	-68.7	-66.9	-68.9	-70.7	-70.5	-70.0	-72.9	-75.6	-73.6	-71.6	-71.4	
31-60	-71.7	-70.2	-66.9	-64.7	-63.3	-67.1	-68.1	-69.6	-70.0	-68.0	-71.8	-71.0	-73.2	-74.6	-77.3	-73.7	-73.9	-72.5	-72.2	-72.4	
61-90	-70.2	-68.0	-67.8	-65.6	-67.4	-73.1	-74.3	-71.7	-71.9	-70.8	-72.8	-68.8	-77.2	-82.2	-83.4	-77.8	-79.7	-80.3	-78.5	-79.3	
91-120	-71.7	-71.7		-71.9	-73.3	-73.8	-74.4		-75.1	-78.0		-66.2	-68.8		-79.6	-84.3	-77.9	-82.6		-81.3	-81.6
121-150	-72.1	-71.9		-74.0	-79.6	-73.3	-77.2		-75.2	-79.5		-63.4	-66.9		-79.0	-83.1	-80.1	-81.6		-80.5	-81.5
151-180	-64.3	-63.9		-72.4	-79.3	-64.5	-70.2		-74.9	-78.2		-64.5	-67.1		-78.2	-81.5	-76.6	-77.5		-79.6	-80.8
Avg. depth	190	83	98.3	231	366																

**Kure Atoll**

**Transect A**

Depth (m)	0030					0300					0530					Day				
	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5	Shb1	Shb2	Shb3	Shb4	Shb5
10-30	-67.9	-68.1	-69.7	-67.4	-66.1	-70.4	-69.6	-68.4	-70.1	n/a	-71.9	-70.9	-71.7	-72.2	-71.7	-73.6	-72.7	-75.9	-72.8	-70.3
31-60	-68.0	-68.5	-68.8	-67.9	-66.9	-71.7	-67.8	-68.4	-70.5	n/a	-72.8	-74.4	-79.0	-81.4	-79.3	-76.4	-74.8	-80.9	-76.9	-76.5
Avg. depth	55.4																			

**Transect B**

Depth (m)	0030					0300					0530					Day				
	Edg1	Edg2	Edg3	Edg4	Edg5	Edg1	Edg2	Edg3	Edg4	Edg5	Edg1	Edg2	Edg3	Edg4	Edg5	Edg1	Edg2	Edg3	Edg4	Edg5
10-30	-71.1	-71.4	-71.7	-71.7	-71.3	-71.1	-71.7	-72.9	-72.3	-71.5	-71.7	-73.0	-72.6	-72.9	-73.9	-73.7	-74.6	-71.6	-72.4	-74.0
31-60	-71.1	-71.0	-71.6	-71.4	-72.7	-72.0	-72.0	-71.6	-70.8	-71.4	-70.0	-73.2	-77.3	-77.6	-78.2	-74.7	-71.2	-70.8	-71.4	-74.7
61-90	-75.4	-76.6	-73.5	-72.6	-72.5	-76.6	-75.9	-68.0	-71.0	-70.1	-68.1	-73.6	-83.1	-82.6	-82.6	-83.4	-81.3	-76.7	-75.1	-81.5
91-120	-73.8	-73.9	-68.4	-68.1	-65.6	-67.2	-68.6	-65.3	-68.8	-67.9	-65.3	-74.7	-77.3	-82.4	-82.5	-84.6	-84.5	-84.3	-79.9	-81.1
121-150	-69.1	-65.4				-62.9	-62.5				-69.9	-68.9				-83.0	-83.0			
151-180	-61.9					-62.4					-69.6					-74.9				
Avg. depth	175	156	127	118	116															

## LITERATURE CITED

- Benoit-Bird, K.J.  
2004. Prey caloric value and predator energy needs: Foraging predictions for wild spinner dolphins. *Mar. Biol.* 145:435-444.
- Benoit-Bird, K.J., W.W.L. Au, R.E. Brainard, and M.O. Lammers  
2001. Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. *Mar. Ecol. Prog. Ser.* 217:1-14.  
Benoit-Bird, K.J., and W.W.L. Au  
2004. Diel migration dynamics of an island-associated sound-scattering layer. *Deep Sea Res.* 51:707-719.
- Benoit-Bird, K.J., W.W.L. Au, R.E. Brainard, and M.O. Lammers  
2001. Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. *Mar. Ecol. Prog. Ser.* 217:1-14.
- Deemer, D.A., and R.P. Hewitt  
1995. Bias in acoustic biomass estimates in *Euphausia superba* due to diel migration. *Deep Sea Res.* 42:455-475.
- Friedlander, A.M., and E.E. DeMartini  
2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar. Ecol. Prog. Ser.* 220:253-264.
- Gal, G., E.R. Loew, A.G. Rudstan, and A.M. Mohammadian  
1999. Light and diel vertical migration: spectral sensitivity and light avoidance by *Mysis relicta*. *Can. J. Fish. Aquat. Sci.* 56:311-322.
- Gliwicz, M.Z.  
1986. A lunar cycle in zooplankton. *Ecol.* 67:883-897.
- Haight, W.R., J.D. Parrish, and T.A. Hayes  
1993. Feeding ecology of deepwater lutjanid snappers at Penguin Bank, Hawaii. *Trans. Am. Fish. Soc.* 122:328-347.
- He, X., K.A. Bigelow, and C.H. Boggs  
1997. Cluster analysis of longline sets and fishing strategies within the Hawaii-based fishery. *Fish. Res.* 31:147-158.
- MacLennan, D.N., and E.J. Simmonds  
1992. *Fisheries Acoustics*. Chapman & Hall, New York.
- Norris, K.S., B. Wursig, R.S. Wells, and M. Wursig  
1994. *The Hawaiian Spinner Dolphin*. University of California Press, Berkeley, CA.
- Reid, S.B., J. Hirota, R.E. Young, and L.E. Hallacher  
1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. *Mar. Biol.* 109:427-440.
- Roger, C., and R. Grandperrin  
1976. Pelagic food webs in the tropical Pacific. *Limn. Ocean.* 21:731-735.
- Skillman, R.A.  
1998. Central pacific swordfish, *Xiphias gladius*, fishery development, biology, and research. NOAA Tech. Rep. NMFS 142, 101-124.



Throne, R.E.

1971. Investigations into the relation between integrated echo voltage and fish density.  
*J. Fish. Res. Bd. Can.* 28:1269-1273.